

# MAMMALIAN SPECIES No. 202, pp. 1-6, 3 figs.

## Desmodus rotundus. By Arthur M. Greenhall, Gerhard Joermann, and Uwe Schmidt

Published 8 April 1983 by The American Society of Mammalogists

### Desmodus Wied, 1826

*Desmodus* Wied, 1826:231. Type species *Desmodus rufus* Wied, by original designation.

*Edostoma* D'Orbigny, 1834. Type species *Edostoma cinerea* D'Orbigny.

*Desmodon* Elliot, 1905:530. An invalid emendation of *Desmodus* Wied.

**CONTEXT AND CONTENT.** Order Chiroptera, Family Phyllostomidae, Subfamily Desmodontinae. The Genus *Desmodus* includes a single living species, *Desmodus rotundus*.

### Desmodus rotundus (Geoffroy, 1810)

#### Vampire Bat

*Phyllostoma rotundum* Geoffroy, 1810:181. Type locality "Paraguay restricted to Asunción" (Cabrera, 1957:92).

*Rhinolophus ecaudatus* Schinz, 1821:168. Type locality "Brasil."

*Desmodus rufus* Wied, 1826:231. Type locality "Fazenda Murebeca," Rio Itabapoana on boundary between states of Espírito Santo and Rio de Janeiro, Brazil.

*Edostoma cinereum* D'Orbigny, 1834. Type locality Santa Corazón, Chiquitos, Bolivia.

*Desmodus d'orbignyi* Waterhouse, 1839:1. Type locality Coquimbo, Chile.

*Desmodus murinus* Wagner, 1840:377. Type locality "Mexico."

*Desmodus fuscus* Burmeister, 1854:57. Type locality "Rio das Belhas," Brazil.

*Desmodus mordax* Burmeister, 1879:78. Type locality "Argentina."

*Desmodus rotundus*, Thomas 1901:194; first use of name combination and spelling now used.

**CONTEXT AND CONTENT.** Context noted above; nine summary above. Two subspecies of *Desmodus rotundus* are recognized:

*D. r. rotundus* (Geoffroy, 1810), see above (*ecaudatus* Schinz, *rufus* Wied, *cineraria* D'Orbigny, *d'orbignyi* Waterhouse, *fusca* Burmeister, and *mordax* Burmeister are synonyms).

*D. r. murinus* Wagner, 1840, see above.

**DIAGNOSIS.** Because the genus *Desmodus* includes only one living species (*Diaemus youngi* here being excluded), the following summary applies to both genus and species: medium-sized (extinct species larger than living species), close-furred bat with rather small, separate, somewhat rounded ears (Fig. 1); lower lip deeply grooved; short muzzle, circummalar ridge suggesting a noseleaf; thumb unusually strong and elongated, slightly longer than hindfoot, three well-developed pads on under surface; forearm and limbs sparsely haired; calcar rudimentary; no tail evident; interfemoral membrane narrow, well haired, not extending to ankle; dental formula, i 1/2, c 1/1, p 1/2, m 1/1, total 20; upper incisors and canines large and knife-like, sharp points of incisors fit into distinct pits in lower jaw behind incisors; lower incisors small, bilobed with distinct central gap (summarized from Anderson, 1972; Goodwin and Greenhall, 1961; Miller, 1907).

**GENERAL CHARACTERS.** Color of dorsal pelage darker than and sharply demarcated from ventral pelage along line from wing to near base of ear; ventral color usually silvery gray. Grayish phase most common but there are also red, gold, and orange phases (Goodwin and Greenhall, 1961). Measurements (in mm) for adults: length of head and body, 69 to 90; length of forearm, 52 to 63; length of thumb, 16 to 20; weight, 25 to 40 g. Females are larger and heavier than males in almost all features (modified from Anderson, 1972; Goodwin and Greenhall, 1961; Husson, 1962; Walker et al., 1975, which also contain longer descriptions and additional measurements).

Measurements and illustrations of skulls (Fig. 2) appear in Anderson (1972), Goodwin (1969), Goodwin and Greenhall (1961), Greenhall (1972), Hall (1981), Husson (1962), and Villa-R. (1966). Photographs of live animals (Fig. 1) appear in Ditmars and Greenhall (1935), Leen and Novick (1969), Schmidt (1978), and Walker et al. (1975).

**DISTRIBUTION.** *Desmodus rotundus* occurs from eastern (north to Tamaulipas) and western (north to Sonora) Mexico (Villa-R., 1966), southward through Middle America and much of South America to Uruguay, northern Argentina, and central Chile (Fig. 3); in the West Indies, vampire bats are found only on Trinidad (Goodwin and Greenhall, 1961). The subspecies *D. r. rotundus* ranges from southern South America north in the Andes to Ecuador; *D. r. murinus* ranges from northern Mexico south to the Amazon basin in South America, including Trinidad (Jones and Carter, 1976).

**FOSSIL RECORD.** Fossils of the genus *Desmodus* have been found from Pleistocene and later deposits. The essential differences between fossil and recent *Desmodus* are in size and proportion, the fossil forms being larger. Cockerell (1930) recorded finding bones of vampire bats, somewhat larger than *D. rotundus*, in a limestone cave in the Terlingua District, about 90 km S Alpine, Texas. *D. rotundus* has also been recovered from Loltun Cave, Yucatan, Mexico (Hatt et al., 1953). A vampire bat taken from Cueva Lamas, near Habana, Cuba, is indistinguishable from *D. rotundus* (Koopman, 1958). A larger vampire bat, *Desmodus stocki* was found in San Josecito Cave, Nuevo Leon, Mexico (Cushing, 1945; Jones, 1958); Tlapacoya, Mexico (Alvarez, 1972); Arredondo, Texas; Potter Creek Cave, Shasta Co. (Hutchison, 1967), and San Miguel Island, Santa Barbara Co., California (Guthrie, 1980). Another large vampire, *Desmodus magnus*, has been recorded from Reddick Cave, Marion Co., and Haile, Alachula Co., Florida (Gut, 1959; Gut and Ray, 1963). Hutchison (1967) claimed that *D. magnus* was not specifically distinct from *D. stocki*, and Kurtén and Anderson (1980) treated it as conspecific with *D. stocki*; they also list the locality in Texas.

Linares (1968) found a fossil *Desmodus* larger than all previously known forms in the Cueva del Guacharo, Monegas, Venezuela. A synopsis of late Pliocene and Pleistocene bats of North America and the Antilles was prepared by Martin (1972).

**FORM.** *Desmodus rotundus* has many specialized skeletal features adapting it for its distinctive feeding habits. The skull (Fig. 2), with its large braincase, is very broad posteriorly and narrows rapidly anteriorly. The rostrum is reduced to a mere support for the enormous incisors and canines (Miller, 1907). The ethmoid bone was described by Allen (1882), the palate by Robin (1881).

The post-cranial skeleton was described, functionally interpreted, and compared with that of other bats by Allen (1896), Altenbach (1979), Mann (1951), Miller (1907), Vaughan (1970),



FIGURE 1. *Desmodus rotundus*, echolocating (photo by U. Schmidt).

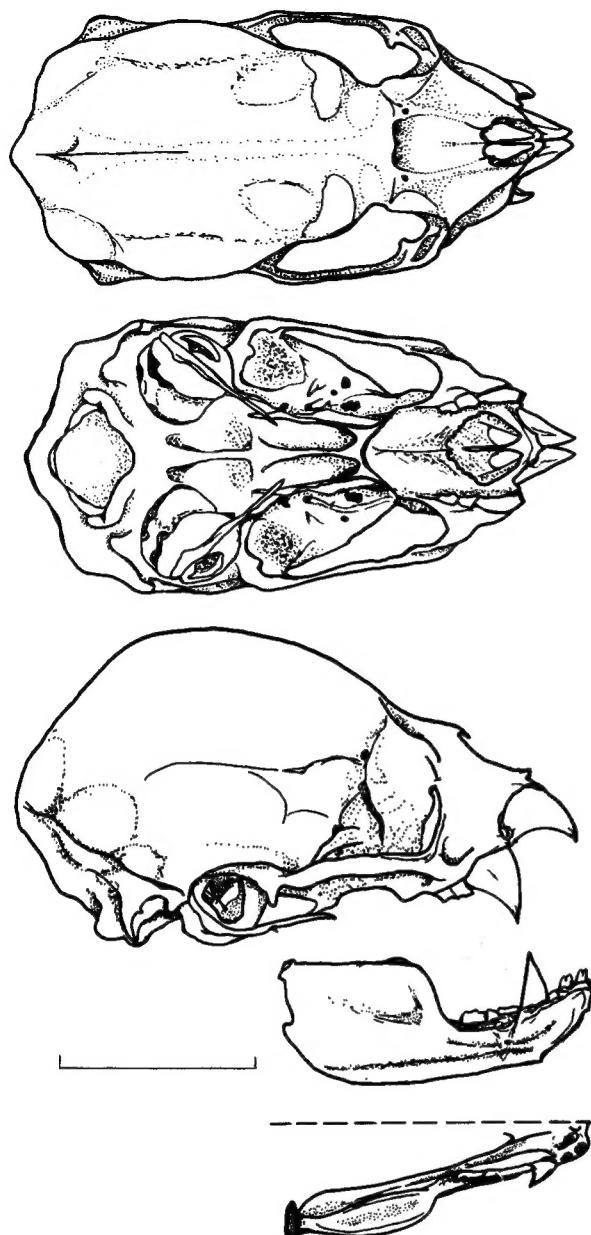


FIGURE 2. Dorsal, ventral, and side views of cranium and mandible, and occlusal view of mandible. Scale represents 10 mm.

and Walton and Walton (1970). The vertebral column consists of 7 cervical, 12 thoracic, 6 lumbar, 5 sacral (fused), and no caudal vertebrae. The atlas and long flexible neck permit the skull to move vertically and laterally. There are 12 ribs (the twelfth rib is less than 1 mm long); the scapula is complex. The strong, well-developed humerus provides a firm base for the alar membrane and together with the elongated thumb, is advantageous for quadrupedal locomotion. The pollex has two phalanges, the distal one bearing a claw. There is one bony phalanx on the second digit. Digits three, four, and five bear three phalanges. The third digit is longest and the phalanges are ossified. The phalangeal formula for the foot and toes is 2-3-3-3-3. Phalanx one of digit one is elongated. There are well-developed claws on all digits which are laterally flattened, arched, and of equal size. All long bones of the leg and wing are deeply grooved for muscle accommodation, especially the tibia, fibula, and femur (Miller, 1907). The calcar is reduced to a wart-like excrescence and is not connected with the interfemoral membrane (Miller, 1907).

Despite many specializations in *D. rotundus*, there is relatively less variation in the muscular system than in that of other bat species (Sterba, 1971). Mann (1951) pointed out that the strong rotary muscles of the forearm and the muscles of the hindlimbs

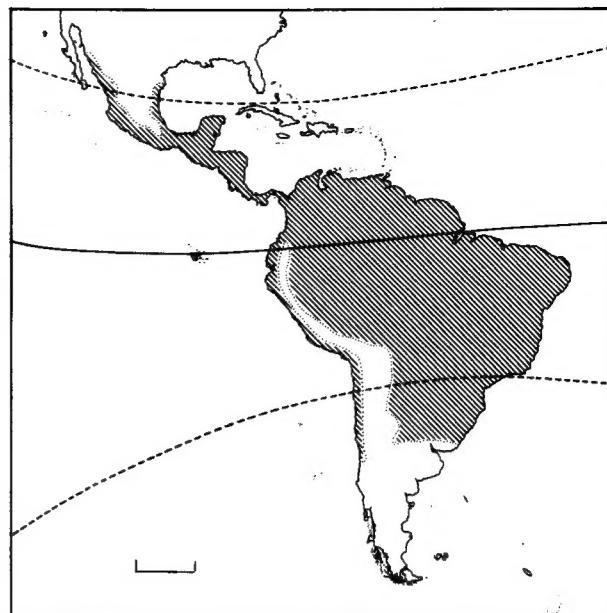


FIGURE 3. Distribution of *Desmodus rotundus* (modified from Schmidt, 1978). Scale represents 1,000 km.

permit quadrupedal locomotion. The masticatory musculature was described by Storch (1968), who compared 19 megachiropterans and microchiropterans.

In *D. rotundus*, the neocortex is better developed than in other bats; the cerebellum is also greatly enlarged (Stephan and Pirlot, 1970). The olfactory centers are generally less developed than in most other phyllostomids but larger than in the insectivorous microchiropterans. The visual areas of the brain are also large (Mann, 1960, 1963a). Yamamoto et al. (1955) noted the large size of the vestibular nuclei. The high degree of encephalization, especially neocorticalization, indicates that the specialized feeding habits demand a good integrative capability of the brain.

**FUNCTION.** The desmodontines are unique among bats in regard to their locomotor skill on the ground. The three pads underneath the thumb are used like a sole. Utilizing high speed photography and electromyographic methods, Altenbach (1979) described in detail the movement of the forelimbs during terrestrial locomotion. The kind of movement on the ground depends on the situation; often there is deliberate walking. To move faster, vampires run or hop. Hopping is sometimes interrupted by short flights. During standing and walking, the shanks and forearms are directed rather vertically, thus supporting the body from below, reducing the effort of maintaining the posture, and allowing the animal to jump into flight. Vampires are able to start flying directly from a position on the ground with folded wings. The jump is powered by a deep adduction of the arms. An additional upward thrust is provided by the flexion of the elongated thumb. A powerful downstroke of the wings produces high thrust and lift to keep the bat airborne. After reaching cruising speed, the flight of *Desmodus* is straight and swift. Body and wing characteristics suggest that they are generalized flyers without special modifications (Altenbach, 1979; Lawlor, 1973; Struhsaker, 1961).

Major senses (sight, olfaction, and hearing) are well developed (Henson, 1970; Mann, 1951, 1960; Suthers, 1970). Echolocation is based on the typical phyllostomid pattern of sound production. Frequency modulated pulses of short duration (0.6 to 1.6 ms) are emitted through the mouth (Schmidt and Schmidt, 1977; Fig. 1). Containing two or three harmonics, sounds range from about 45 to 100 kHz (Griffin and Novick, 1955; Novick, 1963; Pye, 1967; Schmidt and Joermann, 1981).

Vernon and Peterson (1966) compared the hearing of *D. rotundus* with that of *Myotis lucifugus* by measuring cochlear potentials. They reported a higher sensitivity in *D. rotundus*, especially in the frequency range from 100 Hz to 10 kHz. This high sensitivity at lower frequencies may be useful for passive acoustic localization of the prey. The middle ear was anatomically studied by Hinchcliffe and Pye (1969) and Pye and Hinchcliffe (1968).

The eye of *D. rotundus* is in most respects comparable to that of nocturnal rodents (Chase, 1972). Visual acuity is likewise similar

to that of rats (resolution of about 50 ft at 310 lux; Manske and Schmidt, 1976; Suthers, 1966); the lowest light intensity that could be detected by two *D. rotundus* was  $1.8 \times 10^{-7}$  mLambert (Shumake and Caudill, pers. comm.). Vampires are able to distinguish different optical patterns (Manske and Schmidt, 1979); it is likely that they use vision in long range orientation (Suthers, 1970).

The nasal structures (Kämper and Schmidt, 1977) and the rhinencephalon (Mann, 1963b) are remarkably large, and a vomeronasal organ and associated accessory olfactory bulb are present (Mann, 1961). The olfactory acuity is in the range of that of other small mammals and seems to be better than in the insectivorous *Myotis myotis* (Schmidt, 1975; Schmidt and Schmidt, 1978).

The cardiac portion of the stomach forms a tremendously elongated caecum, in which blood is stored during feeding (Huxley, 1865). The extensive vascularization of the tubular stomach (Schultz, 1965) accounts for the rapid water absorption that concentrates the blood meal; 25 percent by volume of blood ingested is excreted in the first hour after feeding (Rosenbaum, 1970; Wimsatt and Guerriere, 1962). Urea from the highly nitrogenous food must be excreted when little free water is present, however, and high levels of urea are produced in the urine. The relation of this unusual excretory ability to feeding habit and ecology of the vampire bat is discussed by McFarland and Wimsatt (1969). Enterobacteria are likely involved in the digestion of the blood. The intestinal flora always contains *Aeromonas hydrophila*, which can decompose the different components of the blood (Müller et al., 1980). *D. rotundus* usually feeds nightly, but can endure fasts for up to 3 days (Crespo et al., 1961; Greenhall, 1970).

**ONTOGENY AND REPRODUCTION.** The female reproductive cycle was studied by Langguth and Achaval (1972), Wimsatt (1954), and Wimsatt and Trapido (1952). The uterus of *Desmodus* was first described by Robin (1881). In *D. rotundus* a single ovum is released at ovulation; there is some evidence that ovaries may function alternately in producing ova in successive breeding cycles (Quintero and Rasweiler, 1974; Wimsatt, 1979). Usually a single young is born of each pregnancy; it may be lodged in either horn of the uterus. Twins were reported by Burns (1972). The gestation period is about 7 months. Seven weeks before birth, the vaginal area becomes pigmented. Birth occurs usually as breech delivery; the placenta is expelled during the first day and is not eaten by the female (Schmidt, 1974).

The newborn is well haired on head and back, the eyes are open the first day (Schmidt, 1978). The milk teeth (di 2/2, dc 1/1, dm 1/2, total 18), present at birth, are in the shape of minute spicules whose chief function seems to be for holding on to the nipple of the mother (De Verteuil and Urich, 1936; Miller, 1896). The permanent upper and lower canines are either present at birth or erupt in 2 to 3 weeks; permanent upper incisors appear at an age of 2 to 5 weeks (Burns, 1972). The birth weight of 5 to 7 g doubles in the first 20 to 25 days. There is rapid development during the first 2 months; after about 5 months growth is completed.

During the first 20 to 30 days, the baby clings nearly continually to the nipple of the mother; up to days 50 to 60 the young is carried by the mother when disturbed. At the same time flight ability is developing. The change from milk to blood nourishment is very slow. The young are suckled up to an age of about 300 days. Starting in the second month, they are fed mouth-to-mouth with regurgitated blood. After about 4 months they accompany their mother to the prey and begin drinking blood by themselves (Schmidt et al., 1980). The recognition of prey by the young and the method of biting are innate. One 6-month-old made a normal bite on a guinea pig and fed from the wound at the first attempt. Another 8-month-old needed 7 days to make its own wound, however, it fed the first day on a wound made by an adult (Schmidt and Manske, 1973). Trapido (1946) observed a female carrying young lift a scab from a sore on a horse after which both drank blood from the wound. In the laboratory young ones that lost their mother were adopted by a female of the colony (Schmidt et al., 1980).

*Desmodus rotundus* probably breeds throughout the year (Wimsatt and Trapido, 1952). In Trinidad gravid and lactating females and females with young were taken during every month of the year, but the highest incidence of young appeared in April and May and in October and November. Goodwin and Greenhall (1961) noted that males are sexually active throughout the year.

**ECOLOGY.** Vampire bats are restricted to areas of warmer climates. In Mexico, they are not found on the Mexican Plateau; in the southern part of the Sierra Madre they occupy higher elevations (2,300 m) than it does northward (1,500 m) (Villa-R., 1966). In El Salvador, *D. rotundus* reaches 1,100 m (Felton, 1956); 1,787 m in Panama (Handley, 1966); 2,594 m in Colombia (Tamm

sitt and Valdivieso, 1962) and 3,800 m in Peru (Malaga Alba et al., 1971; Tuttle, 1970). The northern limit of distribution in Mexico and the southern limit in Chile and Argentina follow the 10°C minimal isotherm for January (McNab, 1969).

*Desmodus rotundus* does not hibernate or estivate. Wimsatt (1962) reported that food consumption and muscular activity increased upon exposure to temperatures between 3 and 5°C. Lyman and Wimsatt (1966) found the vampire bat to be a poor homeotherm with no predictable thermoregulatory capacity. When the ambient temperature decreases, the body temperature is normally held between 33 and 37°C by enhanced motor activity. If cooled down to a body temperature of 20°C, *D. rotundus* is unable to rewarm itself. Wimsatt (1962) also found a sensitivity to high temperatures; 27 to 30°C was suggested as the upper tolerable limit and exposure to 37 to 38°C was lethal.

Vampires roost in natural locations such as moderately lighted small caves, large caves with deep, narrow fissures, "cenotes," and hollow trees. In Costa Rica, Young (1971) found them hiding in tree buttresses. Roosts were described by Dalquest (1955) and Goodwin and Greenhall (1961). Colonies of *D. rotundus* are usually small, numbering between 20 and 100 bats. However, colonies of 500 to 5,000 individuals have been observed (Crespo et al., 1961; Goodwin and Greenhall, 1961; Ruschi, 1952; Villa-R., 1966; Wimsatt, 1959, 1969). Crespo et al. (1961) reported finding males and females segregated within the same roost, although it is more common to find aggregates of different sexes and ages. The groups seem to be stable over long periods, with some members being able to recognize each other (Schmidt, 1978). In some cases there may be multiple roosts among which individuals shift on a more or less opportunistic basis (Wimsatt, 1969). Besides diurnal roosts, there are temporary nocturnal shelters where vampire bats retreat after feeding. These "digesting places" are under bridges, in tunnels, or on trees. Vampire bats are known to share roosts with about 45 different bat species. In Costa Rica, Turner (1975) recorded members of the following genera as inhabiting roosts containing *D. rotundus*: *Micronycteris*, *Glossophaga*, *Carollia*, *Sturnira*, *Saccosteryx*, and *Artibeus*.

Vampire bats commonly forage in an area of 5 to 8 km around the diurnal roost (Crespo et al., 1961); in certain regions this distance may extend to 15 to 20 km (Malaga-Alba, 1954). Within the hunting range certain flyways are regularly used (Greenhall, 1963; Mitchell et al., 1973; Schmidt et al., 1978). Homing experiments suggest that a vampire bat may be acquainted with a large area. In Mexico, two *Desmodus* returned to their roost after 2 and 3 days from a distance of 6 km. One female returned after 5 months from 30 km (Schmidt et al., 1971). In Brazil, Ruschi (1952) marked vampire bats with fluorescent markers and released them 12 to 120 km from the roost. Some returned from 12 km in 2 to 9 h on the same night; from distances of 120 km, some returned after 2 nights.

Non-human predators of *Desmodus* are mainly owls (*Tyto alba*, *Speotyto cunicularia*; Ruschi, 1951) and snakes (*Elaphe flavirufa*, *Constrictor constrictor*, *Bothrops atrox*; Villa-R. and Lopez-Forment, 1966). In Brazil, Villa-R. (1969) observed the carnivorous phyllostomid, *Chrotopterus auritus*, eating a vampire bat. Schmidt et al. (1971) found in Mexico that the birds, *Cassidex mexicanus* and *Psilorrhinus morio*, were able to catch and eat vampire bats after they were released from mist nets in early morning.

Anciaux de Faveaux (1971), Tamsitt and Fox (1970), and Wenzel and Tipton (1966) reviewed the ectoparasites found on *D. rotundus*. Reported genera were: dermanyssid mite, *Radfordiella*; spinturnicid mite, *Periglischrus*; macronyssid mite, *Macronysoides*; sarcopid mite, *Chironyssoides*; argasid tick, *Ornithodoros*; ixodid ticks, *Ixodes* and *Amblyoma*; trombiculid chiggers, *Euschoengastia*, *Trombicula*, and *Nycterinastes*; siphonapterid fleas, *Polygenis*; nycteribid bat flies, *Basilia*; streblid bat flies, *Trichobius*, *Megistopoda*, *Speiseria*, *Trichobioides*, and *Strebla*.

Endoparasites include the protozoan, *Grahamella brumpti*, reported from Peru by Stiles and Nolan (1931), and the nematode, *Biacantha desmoda*, described from Trinidad (Wolfgang, 1954). Hoare (1972) listed the following trypanosomes from *D. rotundus*: *Trypanosoma cruzi*, *T. vespertilionis*, *T. pessoui*, and *T. megadermae*. Blood smears from bats with trypanosomes failed to infect the triatomine bugs (*Rhodnius*) according to Hoare (1972).

The mode of nutrition in *D. rotundus* involves a danger for the prey and is of importance for public health. Whereas the loss of blood is not critical, at least for large animals, the prey is damaged by infection of the wounds with hematophagous arthropods and screw worms and by transmission of diseases. The most important diseases are some trypanosomiasis such as "murrina" (*Trypanosoma hippicum*) and "mal de caderas" (*Trypanosoma equinum*) and paralytic rabies. As transmitters of paralytic rabies (Derriengue)

to livestock, vampire bats cause considerable economic damage in Latin America. According to Pawan (1936) some individuals of *D. rotundus* appeared to develop resistance to rabies. However, vampire bats are not long term "carriers" because the bats die when they contract rabies. Experimentally, vampire bats also have transmitted the viruses of foot and mouth disease and yellow fever. The vampire bat is controlled by different techniques as has been discussed by Linhart (1975), Schmidt (1978), and Turner (1975).

**BEHAVIOR.** Presently the food of *Desmodus* appears to consist mainly of the blood of livestock (cattle, equines, goats, sheep, pigs), poultry, and occasionally man. Based on precipitin tests of stomach contents, Greenhall (1970) reported that, in addition to domestic animals, the bats had also fed upon a number of unidentified wild animals. The favorite sites for biting on bovines, equines, sheep, and goats are the shoulders, neck, base of horns, base of ears, snout, elbows, legs, tail, vulva and anus. Pigs are bitten on the nose, ears, and teats; poultry may be attacked on combs, neck, under the feathers, legs, undersurface of toes, and anus. The typical bite of *D. rotundus* has been described by many biologists including Beebe (1927), Ditmars and Greenhall (1935), and Townsend (1927). After selection and preparation of a wound site (Clark, 1948; Greenhill, 1972), a piece of the skin is bitten off (Schmidt and Manske, 1973) or a wound is gouged using only the upper jaw (De Verteuil and Urich, 1936). Detailed mechanics of biting were described by Storch (1968). If the blood flow is not sufficient, another bite is made at the same site (Mann, 1951), sometimes deep into the muscle tissue (Goodwin, 1934; Greenhall, 1972), or the wound is deepened with the tip of the tongue. The tooth sharpening mechanism suspected by Greenhall (1972) was confirmed by Phillips and Steinberg (pers. comm.), who suggested that enamel agenesis allowed for a more efficient tooth cutting edge. Mann (1950) first described two channels on the underside of the tongue, between the lingua and sublingua, where blood is drawn into the mouth by movements of the tongue. Observations of 13 *Desmodus* feeding on neck sites of cattle yielded a feeding time of 9 to 40 min (Greenhall et al., 1969). Crespo et al. (1961) and Sanborn (1931) reported seeing up to eight vampire bats feeding on the same animal; Schmidt et al. (1970) observed seven *D. rotundus* feeding from the same wound, one after another, within a 3-h period. Wimsatt and Guerriere (1962) estimated that wild vampire bats may drink an average of 20 ml per day. After feeding ceases, the wound continues bleeding for a considerable time as the saliva of *D. rotundus* contains several anticoagulants (Cartwright, 1974; Hawkey, 1966, 1967).

The social organization of *D. rotundus* is still poorly known. In the laboratory, one male always is dominant and repulses other males from the females. The fighting usually is ritualized, the opponents knocking each other with folded wings (Schmidt and Van de Flierdt, 1972). A variety of social calls is emitted in acoustic communication (Sailier and Schmidt, 1978).

**GENETICS.** Baker (1970, 1973) and Forman et al. (1968) studied the chromosomes of *D. rotundus*. The diploid number is 28 and the number of autosomal arms (FN) is 52. All autosomes are biaxed and, except for one medium-sized pair of subtelocentrics, are metacentrics or submetacentrics. The X chromosome is the largest submetacentric. The Y chromosome usually appears as a minute acrocentric; however, in one specimen from Trinidad it had a biaxed appearance.

According to its chromosomal morphology, *D. rotundus* is closely related to *Diphylla* (Bass, 1978). Using serum electrophoreses and albumin immunology, Honeycutt et al. (1981) found a striking similarity of the albumins of *Desmodus* and *Diaemus*. This is in agreement with morphological data (Smith, 1976).

**REMARKS.** A partial bibliography of literature on the vampire bat, with some 626 references, was compiled by Linhart (1970); different aspects of the biology of *D. rotundus* were reviewed by Schmidt (1978).

The tradition of the supernatural vampire was traced by Ditmars and Greenhall (1935). According to Dalquest (1953) vampire attacks on humans in San Luis Potosi, Mexico, were attributed to witches (brujas) by country people. Villa-R. (1966) discussed the association of the pre-Columbian Mayas and Aztecs with the vampire bat.

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MAMMALIAN SPECIES No. 202, pp. 1–6, 3 figs.

## Desmodus rotundus.

Published 15 December 1983 by The American Society of Mammalogists

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### ERRATUM

Michael R. Seidel was mistakenly omitted as an author on *Mammalian Species* account no. 202. The correct citation should read:

Greenhall, A. M., G. Joermann, U. Schmidt, and M. R. Seidel. *Desmodus rotundus*. Mamm. Species, 202:1–6.